THEMATIC COLLECTION: INTRODUCTION

Why Primates? The Importance of Nonhuman Primates for Understanding Human Infancy

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We introduce the thematic collection by noting some striking similarities in the cognitive abilities of human infants and nonhuman primates. What are the implications of these similarities for our comprehension of human infant cognition? After providing a brief historical and conceptual background on comparative behavioral research, we discuss how nonhuman primate research has impacted theories of core knowledge, domain specificity, and language. We conclude by previewing the articles comprising this special issue of *Infancy*.

As readers of *Infancy* are surely well aware, young infants are capable of some remarkable cognitive feats. Infants can, for example, add and subtract small numbers of objects (e.g., Wynn, 1992), keep track of statistics in running speech streams (e.g., Saffran, Aslin, & Newport, 1996), learn rudimentary "algebraic" rules (e.g., Marcus, Vijayan, Bandi Rao, & Vishton, 1999), make accurate predictions about the physical trajectories of moving objects (e.g., Baillargeon, 2004; Spelke, Breinlinger, Macomber, & Jacobson, 1992), discriminate between animate

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and inanimate objects (e.g., Johnson, Slaughter, & Carey, 1998), and recognize the intentions behind an agent's actions (e.g., Behne, Carpenter, Call, & Tomasello, 2005; Woodward, 1998). Remarkably, all of these abilities come online in the absence of any explicit training and often before the infant has ever uttered a single word.

Although infants' cognitive achievements are undoubtedly impressive, young humans are not the only organisms to develop sophisticated cognitive skills in the absence of language and formal teaching. Parallel lines of research with non-human primates (hereafter primates) have demonstrated that, like human infants, our closest evolutionary relatives possess a number of remarkable cognitive capacities. Lemurs (*Eulemur mongoz*) can add and subtract small numbers of objects (e.g., Lewis, Jaffe, & Brannon, 2005). Tamarins (*Saguinus oedipus*) can track statistics in speech streams (Hauser, Newport, & Aslin, 2001; Newport et al., 2004) and learn rudimentary grammatical rules (Hauser, Weiss, & Marcus, 2002). Rhesus monkeys (*Macaca mulatta*) make accurate physical predictions about object motion (e.g., Santos & Hauser, 2002) and understand some of the physics behind simple tools (e.g., Santos et al., 2004). Chimpanzees may recognize the intentions behind an agent's actions (Call, Hare, Carpenter, & Tomasello, 2004).

At first blush, these findings seem somewhat paradoxical. Across many studies, human infants and adult primates appear to share nearly identical cognitive profiles and yet, unlike infants, primates do not go on to acquire language, learn calculus, master quantum mechanics, or develop elaborate material technologies. What, then, are the underlying cognitive differences between infant primates and humans that are responsible for the eventual disparity between adult primates' and humans' conceptual achievements? How do human infants go beyond their similarly endowed primate cousins to achieve the impressive cognitive feats that adult humans uniquely perform?

This *Infancy* thematic collection is devoted to the ways in which research with nonhuman primates can ultimately inform these developmental questions. Each of the articles in this collection is an attempt to explore a different aspect of human infant development through the window of primate behavior. The articles in this collection span a number of important topic areas in infant development, including the emergence of infants' early object concepts (Santos, Seelig, & Hauser, 2006/this issue), the emergence of infants' numerical reasoning capacities (Cantlon & Brannon, 2006/this issue), the development of a sense of self (Bard, Todd, Bernier, Love, Leavens, 2006/this issue), the development of affective and arousal systems (Mizuno, Takeshita, & Matsuzawa, 2006/this issue), and the mechanisms underlying human language acquisition (Weiss & Newport, 2006/this issue). Before turning to these articles, however, we briefly sketch how primate research can constrain theories of human development, highlighting the

ways in which comparative studies can inform developmental problems of particular relevance to infancy researchers.

THE IMPORTANCE OF A PRIMATE COMPARISON: HISTORY AND INSIGHTS

The idea that work with nonhuman primates can constrain theories of human development is undoubtedly an old one in the field of psychology (see Tomasello & Call, 1997, for an elegant historical review). Darwin himself was one of the first to recognize that the study of primates might provide important insight into the nature of human behavior, but it was only decades later that the renowned American psychologist, Robert Yerkes, began perhaps the first systematic study of psychological processes in other primate species.[1] Yerkes (1943/1971) argued that primates may serve as an informative window into human psychology in the absence of culture and formal teaching. In his own words, "the study of other primates may prove the most direct and economical route to profitable knowledge of ourselves, because, in them, basic mechanisms are less obscured by cultural influence" (p. 3).

To achieve this end, Yerkes established a laboratory of primate studies that could host and provide training for a new generation of primate researchers. This new center's training eventually resulted in a number of the earlier and most famous studies comparing human and primate development, including Kellogg and Kellogg's (1933) cross-fostering studies of the chimpanzee Gua and Hayes and Hayes's (1951) attempt at teaching the chimpanzee Viki to use human speech. These early cross-fostering studies were founded in part on the logic that primates (particularly, closely related chimpanzees) can be used as a tool to explore how experience gives rise to important human developmental achievements (e.g., language acquisition). These studies also address the extent to which some human cognitive achievements are unique and thus may never be attained by members of other species. Such logic has endured and remains a driving force behind many contemporary comparative primate studies.

Early psychologists were not the only scientists to recognize the importance of comparative work in constraining developmental questions. Perhaps the most important insights into the role of primates in the study of human development came from the field of biology and, in particular, the early ethological tradition. The

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[1]It is important to note that another German psychologist, Wolfgang Kohler, began a similar comparative investigation of chimpanzee psychology around the same time as Yerkes. Nevertheless, it was Yerkes's work and facilities that generated the most furor into the establishment of the scientific study of primates here in the United States.

Nobel Prize-winning ethologist Tinbergen (1952) offered a framework guiding the study of behaviors that argued for the importance of connecting comparative work with other areas of inquiry. Tinbergen argued that to fully understand a behavior one must study it from at least four different levels of analysis.[2] Tinbergen's first two levels of analysis—the mechanistic and ontogenetic—are those most closely tied to the daily goals of many infancy researchers. The *mechanistic* level involves determining the underlying mechanisms—both psychological and biological—that give rise to a particular behavior. The *ontogenetic* level involves determining the developmental trajectory of a particular trait. At this level, one must consider both the initial precursors to a given trait and then how environmental factors shape the development of that trait over an individual's life course.

The remaining two levels of ethological analysis—the phylogenetic and functional levels—are somewhat less common approaches among developmental psychologists but no less important or insightful. The *phylogenetic* level involves examining the phylogenetic history behind a given trait. Like the ontogenetic level of analysis, a phylogenetic study of a particular trait involves looking both at the origins of a trait—in this case, origins over evolutionary time—and the changes to that trait over time, across the primate ancestry. The most transparent contribution of primate work to the study of infant development is realized at this phylogenetic level. Because behaviors do not fossilize over time, the best method for inferring how the behaviors changed over evolutionary time is to investigate whether or not homologous behaviors are present in other closely related species. Applying this logic to the study of human development demonstrates the importance of primate work specifically. Because primates are our closest living relatives, primate research is particularly relevant for making claims about the evolutionary history of a trait or behavior observed in humans. To take one example, newborn human infants respond with positive facial reactions to sweet tastes, and negative facial reactions to bitter tastes (Steiner, 1973, 1979). Several nonhuman primate species (including great apes, Old World monkeys, and New World monkeys) have been observed to produce similar reactions to sweet and bitter types of food (Steiner, Glaser, Hawilo, & Berridge, 2001). The ubiquitous nature of these affective reactions in primates (including humans) suggests that the behaviors are phylogenetically related and consequently represent true homologues.

Tinbergen's final level of analysis, the *functional* level, is perhaps the most neglected way of thinking about the development of human cognition. A functional level of analysis involves determining the adaptive function of a particular cognitive trait, the way in which it affected survival and reproductive success over evolutionary history. In many cases, the function of a trait or behavior may appear

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[2]Note that these levels are not completely orthogonal, as some analyses may overlap different levels. Likewise, there is no hierarchy of importance presupposed by these levels of analysis.

to be transparent with respect to current utility. However, assessing current function does not always inform us about why the trait originally evolved, particularly in the case of modern humans, who have undoubtedly strayed from the ancestral environment in which they evolved. As such, a trait's true functional basis may be somewhat obscured in the modern environment, which may limit developing new theories about both the reason a trait was designed and constraints on how it may have developed. Adopting a comparative cross-primate approach, then, may yield significant insights as to the original function of existing traits.

An interesting example of this phenomenon is demonstrated in discussions about the origins of the shape of the human vocal tract. The human vocal tract is anatomically positioned much lower than in other primates, precluding the ability to breathe and swallow simultaneously.[3] One of the benefits from the shape of the human vocal tract is that it provides the tongue with sufficient degrees of freedom to support the production of complex sounds necessary for language (Lieberman et al., 1969). This finding naturally led to the theory that the descent of the vocal tract was a feature that evolved to support language production (see Fitch, 2000). Recently, however, scientists have begun studying the vocal tracts of other species. This work has lead to new functional theories about the descent of the human vocal tract. Curiously, humans are not the only species with a descended larynx. The position of the larynx in a number of deer species is similar to that observed in older humans. Work by Fitch and Reby (2001) has observed that such descended positions allow male deer to produce vocalizations that mask their real body size, projecting a pattern of formants consistent with larger animals. Functionally speaking, these vocalizations may attract females interested in larger mates or intimidate rivals by exaggerating their perception of size. A similar type of exaggeration is evidenced in other species (notably in birds) with unusually elongated trachea (Fitch, 1999). Applying these findings to humans has led to a new theory about vocal tract shape, namely that the descent of the vocal tract in humans may have been related to the function of broadcasting information about an individual's body size. This idea is further supported by the secondary descent of the vocal tract during puberty in males (Fitch & Giedd, 1999), which occurs after individuals have already mastered the complexities of vocal production required for normal adult speech. Although this theory may not be a complete account of why the vocal tract is descended in humans (see Pinker & Jackendoff, 2005), it leads to an interesting series of predictions concerning the development and structure of human vocal production. Thus, this example demonstrates how, at the functional level, comparative research can fuel new intuitions about the functional design of human traits and the nature of their development.

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[3] The human vocal tract actually descends during the course of development. At around 3 months of age the vocal tract begins its descent, which reaches the adult position at roughly 3 to 4 years of age (Fitch, 2000).

Having provided a brief historical background, we now turn to two areas in which comparative research with primates has been influential in the study of infant development: the nature of infant core knowledge and questions concerning the role of language in cognitive development.

Core Knowledge and Domain Specificity

One area in infancy research in which primate studies have come to the forefront concerns the debate surrounding the nature of the infant's core knowledge (see Spelke, 2000). The idea of core knowledge is predicated on the view that human cognition develops in part though a series of domain-specific systems that operate over a restricted set of inputs (see Carey & Gelman, 1991; Hirschfeld & Gelman, 1994; Keil, 1989). Accordingly, the core knowledge theory maintains that infants are born into the world possessing a number of specialized mechanisms dedicated to representing ecologically relevant entities and events—problems such as representing objects (e.g., Spelke et al., 1992), recognizing agents (e.g., Leslie, 1994; Spelke et al., 1994), reasoning about numerical information (Feigenson, Dehaene, & Spelke, 2004; Hauser & Spelke, 2004), and navigating through space (Spelke, 2002). These innately endowed core mechanisms are thought to facilitate infants' ability to solve relevant environmental problems by constraining, in advance, the types of solutions to be considered. In this way, the idea of core knowledge dovetails nicely with ethological views surrounding the origins of cognition in nonhuman animals (see Gallistel, 1990; Hauser, 2000). Like infant core knowledge theorists, animal behaviorists have argued that species-specific selective pressures can result in innately directed learning mechanisms for solving specialized cognitive problems such as spatial navigation (e.g., Emlen, 1975), predator recognition (e.g., Cheney & Seyfarth, 1990), and foraging (e.g., Santos, Hauser, & Spelke, 2001).

A vital component of the core knowledge view, then, is that infants' early capacities are not arbitrary; instead, core knowledge mechanisms should reflect solutions that are useful for solving a very particular set of problems faced during our recent evolutionary past. For this reason, paying close attention to the problems facing our closest living primate relatives can provide important cues to identifying core systems in human infants. More important, however, primates, like human infants, can be used as a viable test case for hypotheses about core knowledge. Primates and humans face many of the same evolutionary dilemmas, the same problem domains for which innately specified domain-specific solutions might be most useful. Consequently, it is reasonable to presume that adult primates may share some of the core systems observed in human infants. This assumption has been borne out in the past decade, with primate researchers identifying a number of domains in which human infants and primates seem to share similar cognitive machinery (see reviews in Hauser & Spelke, 2004; Spelke, 2000).

Not surprisingly, then, infancy researchers have already gained considerable insight into the core domains of human knowledge by studying both human infants and nonhuman primates in concert. One marvelous example of the value of this collaboration can be seen in the domain of numerical knowledge (see reviews in Feigenson et al., 2004; Hauser & Spelke, 2004). Infant researchers have long been interested in the extent to which human infants enter the world prepared to reason about numerical information and the extent to which human infants and adults share mechanisms for representing natural number. Such interest has led to a great deal of empirical work, much of which suggests that the conceptual basis for numerical understanding in both human infants and adults draws from two different core knowledge numerical systems: one for representing large approximate values (often referred to as an accumulator or analogue magnitude system; see Brannon & Roitman, 2003; Feigenson et al., 2004), and one that more precisely represents smaller numerical values (often referred to as the object file system; see Feigenson & Carey, 2003; Hauser, Carey, & Hauser, 2000).

To test this two-system view, primate researchers have begun to explore whether the same two core numerical systems are spontaneously available to untrained primates. In doing so, primate researchers have been able to utilize some of the same types of tasks that have been used to explore similar questions in human infants (e.g., Hauser et al., 2000; Lewis et al., 2005; Santos, Barnes, & Mahajan, 2005), allowing for a direct comparison across infant and primate populations. For example, using a manual search task similar to those employed by human infants (e.g., Feigenson & Carey, 2003), Lewis and colleagues (2005) established that untrained mongoose lemurs are capable of discriminating large numbers of objects. This ability appears to be constrained by a Weber signature, perfectly corresponding to research conducted with 6-month-old infants, which has shown a similar constraint (Xu & Spelke, 2000). The smaller, more precise, number system has also been demonstrated in untrained primates (although the nature of this system's operation in primates has remained somewhat more controversial; see Lewis et al., 2005). Using an expectancy violation looking paradigm modeled after that of Wynn (1992), Hauser and colleagues have demonstrated that free-ranging rhesus monkeys can successfully add smaller numbers of objects (e.g., recognizing that $2 + 1 = 3$ but not 2), but fail to discriminate larger numbers of objects presented at equivalent ratios (e.g., $4 + 2 = 6$ but not 4; see Flombaum, Jonge, & Hauser, in press). Rhesus monkeys also fail to precisely discriminate large numbers in a two-choice search task (e.g., Hauser et al., 2000). Like human infants tested on a similar task (Feigenson et al., 2002), rhesus monkeys succeed in making precise numerical discriminations when presented with comparisons between small numbers of objects (e.g., 1 vs. 2, 2 vs. 3), but fail when the number of items in one of the two search locations falls outside the object file range (e.g., 4 vs. 5). Again, these results have been argued to indicate that monkeys share infants' capacity-limited core system for reasoning about

small numbers of objects. In this way, studies with primates have aided infancy researchers in determining the extent to which the capacities observed in human infants truly represent two separate systems for core number reasoning.

Language: Its Uniqueness and Role in Human Cognition

One of the great mysteries facing researchers interested in infant language acquisition is the fact that only human infants are capable of successful acquisition. No primates outside of the human species have ever mastered language, and no other primate communication system—including that of the very closely related chimpanzee—is as complex and sophisticated as human speech. For this reason, primates (as well as other nonhuman animals) can provide an important counterpoint for work with prelinguistic infants. When investigators contrast the performance of human adults and infants, they are essentially comparing two types of brains: ones that have a fully functioning linguistic system, and ones that are in the process of developing such a system. By adding a third subject population—primates— infancy researchers gain a critical third comparison point in their comparative arsenal: a brain that does not have a fully functioning linguistic system and never will.

In this way, primates often provide the best yardstick for measuring which cognitive developments truly require linguistic competence, be it fledgling or fully developed, and which do not. Take, for example, recent developmental debates concerning how and when infants develop the capacity to represent object kind information (e.g., Xu & Carey, 1996). A growing body of work has demonstrated that human infants undergo a striking shift in their ability to represent hidden objects at the time they begin learning words around 12 months of age (Xu & Carey, 1996; Xu, Carey, & Quint, 2004; but see Needham & Baillargeon, 2000); rather than simply attending to an object as a spatiotemporal unit, infants seem to begin representing objects as different ontological kinds, categories like "duck" and "truck." Xu and her colleagues have hypothesized that infants' emerging kind representation abilities stem directly from their newfound language capacities. In particular, Xu and colleagues have argued that learning a word for an object allows infants to begin reasoning about objects using kind representations. In support of this, Xu (2002) observed that preverbal infants perform better on kind individuation tasks that involve verbal labels but not other salient auditory cues (e.g., emotional vocalizations). Her results provide strong suggestions that language (specifically, words) might be necessary for individuating objects in terms of ontological kind. In contrast to this conclusion, however, comes work using similar kind individuation experiments with primates (see Munakata et al., 2001; Phillips & Santos, under review; Santos, Sulkowski, Spaepen, & Hauser, 2002; Uller, Xu, Carey, & Hauser, 1997). Rhesus monkeys, which of course lack the capacity to understand words, succeed in representing objects in terms of their kind in tasks identical to those involving human infants. These successes in the absence of language suggest that,

although language learning may aid infants in coming to reason about ontological kinds, word learning cannot be necessary for kind representations. In this example and others, then, primates can serve as a useful tool for determining whether developing cognitive skills are truly reliant on language acquisition or whether such skills could instead emerge even in the absence of linguistic competence.

Work with nonhuman primates is also one of the best ways to constrain hypotheses concerning how human infants come to be such accomplished linguists in the first place. Perhaps the most fundamental issue in human language research is the question of whether the mechanisms that allow infants to learn language evolved specifically for language use (and are consequently uniquely human) or whether these mechanisms are built from domain-general parts that might be shared with other species. In light of this quest, adopting a comparative approach can be useful as a means of testing whether particular abilities are indeed unique to humans. Although primates never come to perceive language like a word-learning child, they do share some core computational abilities that are necessary for language and speech perception (e.g., Hauser et al., 2001; Kuhl & Miller, 1975; Liberman, Harris, Hoffman, & Griffith, 1957; Ramus, Hauser, Miller, Morris, & Mehler, 2000; Terrace, 2005). Observing that primates share the very mechanisms that infants use in the service of language acquisition provides evidence that the mechanisms under question are not specific to language per se, and may have evolved for more general computational problems. In contrast, identifying mechanisms that are present in human infants but absent in primates lends support for a uniqueness claim, suggesting that the mechanisms in question may be specific to the task of language learning.

Although this logic is rather straightforward, in fact, many uniqueness claims have been made in the absence of gauging nonhuman performance. The initial discovery that adult and infant humans categorically perceive phonemic contrasts (Eimas, Siqueland, Jusczyk, & Vigorito, 1971; Liberman, Harris, Hoffman, & Griffith, 1957), for example, led to the hypothesis that this ability was related to language and consequently was uniquely human. In contrast to this uniqueness claim, studies of chinchillas (Kuhl & Miller, 1975), macaques (Kuhl & Padden, 1983), and birds (Kluender, Diehl, & Killeen, 1997) have demonstrated unequivocally that at least some nonhuman animals also perceive speech sounds categorically, suggesting that this feature may be a general property of the mammalian (and avian) auditory system. Similarly, a number of philosophers hypothesized that human infants are the only creatures that come to communicate about the world referentially. Again, however, research with primates (e.g., Cheney & Seyfarth, 1990) and even other nonhuman species (e.g., Marler, Dufty, & Pickert, 1986; von Frisch, 1967) has shown that referential communication appears to be an ability shared more broadly across the animal kingdom. In this way, claims about language uniqueness can often best be substantiated through continued comparative research (see Hauser, Chomsky, & Fitch, 2002; Pinker & Jackendoff, 2005).

THIS ISSUE

This *Infancy* thematic collection represents an attempt to bring together a number of different perspectives on the ways in which primate research has and will shape future insights into infant development. Although *Infancy* routinely publishes studies involving primate comparisons, our goal in this collection is to synthesize research from a number of independent investigators working on a range of different theoretical questions and using a variety of different empirical approaches.

The first of these articles, authored by Santos et al. (2006/this issue), examines whether primates share the unexpected dissociation observed in human infants' performance on looking and searching measures of object knowledge. Santos and colleagues find that human infants are not alone in their poor search task performance; adult tamarin monkeys seem to do poorly on tests of solidity that involve searching for hidden objects, even though they perform well on similar conceptual problems when tested using looking measures. The observation that infants and tamarins share this methodological dissociation challenges many of the explanations put forth by infancy researchers, and thus poses additional questions about the origins of this peculiar, yet highly reliable, aspect of infants' performance.

The second article in this issue, authored by Cantlon and Brannon (2006/this issue), also compares the way in which humans and primates come to represent objects, but this time, with an eye toward the capacity to enumerate objects. More specifically, Cantlon and Brannon investigated whether rhesus monkeys can spontaneously establish abstract numerical representations, ones that apply over heterogeneous sets of stimuli. These researchers observe that rhesus are able to abstract over heterogeneous sets of stimuli even in conditions in which they were not originally trained to do so. Their results provide some of the best evidence to date that some species of monkeys, like linguistically savvy humans, can represent numerical information abstractly rather than on the basis of the items' features or objective perceptual characteristics.

The third article, authored by Bard et al. (2006/this issue), attempts to disentangle the controversy surrounding the now-infamous mirror-self recognition test through the use of a truly comparative-developmental approach—one that tests both human and primate infants using similar methodologies. Bard and colleagues' results present an important methodological caveat: When truly comparable methods are used across primates and humans, similar abilities can sometimes be observed.

Mizuno, Takeshita, and Matsuzawa (2006/this issue) present an observational study on the nocturnal behaviors of infant chimpanzees, comparing their development to analogous human infant behaviors. This research represents one of very few studies of spontaneous activity during sleep periods in infant chimpanzees. In fact, it is unique in being the only laboratory study to date that studies the nocturnal behaviors of infants reared by their own mothers rather than by humans. The

results are equally novel, as the authors report the first ever evidence that, like human infants, young chimpanzees produce neonatal smiling during rapid eye movement sleep. This type of smiling diminishes after 2 months, replaced by social smiling (smiling with eyes open while facing another individual). The time course of this change, as well as other behavioral changes reported in the article, follows a similar developmental trajectory as has been reported for human infants. Thus, the authors end by speculating on the implications of the similar developmental shift in 2-month-old humans and chimpanzees.

In a summary article, Weiss and Newport (2006/this issue) discuss the impact of the comparative approach on the study of the cognitive mechanisms that facilitate language acquisition in humans. They provide a brief historical and methodological context for recent developments in comparative language research, and then critically explore the influence of recent untrained behavioral studies that have been central to some of the most current, and contested, theories of language evolution. One point of emphasis is the need to look beyond surface similarities in behavior and examine whether underlying cognitive functions and computational primitives are in fact similar across species. They conclude with a discussion speculating on the important future directions for this field of study.

It is our hope that this thematic collection will contribute to a more nuanced view of the importance of primate research for developmental psychology and that it may inspire a new generation of collaborations between primate and infant researchers. As we think Darwin himself would have agreed, such a broadly comparative developmental approach will surely provide the best perspective on how human infants grow up to surpass other primates and become such linguistically savvy, cognitively impressive human adults.

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